

GAS EXCHANGE RATES OF THREE SUB-SHRUBS OF CENTRAL TEXAS SAVANNAS

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ABSTRACT

Savannas are open communities with a woodland and grassland phase. Some species are restricted to one phase or the other with some in both. The central Texas Edwards Plateau is mainly a savanna community with an east to west rainfall gradient and a tree density gradient with both factors being reduced in the west. We examined gas exchange rates of sun and shade leaves of three perennial species of Asteraceae, *Simsia calva* (bush sunflower), *Wedelia texana* (hairy wedelia), and *Brickellia cylindracea* (brickell-bush). Maximum photosynthetic rates (A_{\max}), light saturation points (L_{sat}), ambient light levels, leaf mass per area, leaf conductance, and transpiration rates (E) for sun leaves were significantly greater than shade leaves for all three species. Mean A_{\max} rates were 32.8, 23.2 and 21.2 $\mu\text{molCO}_2/\text{m}^2/\text{s}$ for sun leaves of *S. calva*, *W. texana* and *B. cylindracea* respectively. For shade leaves, rates were 21.3, 15.2 and 12.9 $\mu\text{molCO}_2/\text{m}^2/\text{s}$ respectively for the same species. Mean R_d (dark respiration) rates were 3.00 $\mu\text{molCO}_2/\text{m}^2/\text{s}$ for sun leaves and 1.1 $\mu\text{molCO}_2/\text{m}^2/\text{s}$ for shade leaves of *S. calva*. R_d rates for sun and shade leaves of *W. texana* and *B. cylindracea* were mostly lower but only significantly different for *B. cylindracea*. There were no significant differences between sun and shade leaves for the initial slope or quantum yield for any of the species. Leaf mass per area was greater for sun leaves of all species. A_{\max} rates for sun leaves were high as expected for sun plants, but A_{\max} rates for shade leaves were fairly high as well, probably because of the relatively open nature of the sub-shrub canopy. Most factors measured were high and suggest that these plants are sun plants or facultative species. These measurements would help explain why these species are present in the full sun, open grassland phase of these central Texas savanna communities and not below the woodland canopy where their growth and survival would be reduced because of lower light levels.

Key Words: CO_2 uptake, photosynthesis, savannas, shade leaves, sun leaves.

Composition and structure of grassland communities Worldwide have changed and are continuing to change (Bond 2008; Van Aiken 2009). These transformations include grasslands from California through Arizona, New Mexico and central Texas (Van Aiken and McKinley 2008; Maze 2009). Many of the changes involve the encroachment or invasion of a few woody species; however, as many as 10% of the herbaceous species in southwestern arid or semiarid grasslands are invaders from all over the World (Van Aiken 2009). The composition and structural changes have occurred because of modifications in the level and kind of herbivory, other disturbances and the reduced frequency and intensity of grassland fires. However, some still suggest that global phenomena such as elevated levels of atmospheric CO_2 and concomitant temperature increases are the primary cause of the changes in these grasslands (Van Aiken 2009). Regardless of the specific cause or causes, the mechanisms directing or driving the conversion in these grasslands have been difficult to identify.

Simple as well as complex gradients of rainfall, temperature, light, soil resources, biotic factors or combinations occur throughout the world, determining to a large extent the kind of communities and species of plants that are present in given areas (Begon et al. 2006). Woody plant density and cover change along rainfall gradients with desert shrubs increasing on the dry end of the gradient, woodlands or forests on the wetter end with grasslands or savannas in between (Boardman 1977; Larcher 2003; Breshears 2008). This type of gradient occurs, proceeding from west to east, on the Edwards Plateau in central Texas (Van Aiken and McKinley 2008). Although the structure of some of the communities along this rainfall gradient have been described (Van Aiken and McKinley 2008; Van Aiken and Smeins 2008; Wayne and Van Aiken 2008), the reasons that various species occur in defined places and at certain densities along this gradient are not clear and predicting the dynamics of this biphasic system is challenging (House et al. 2003).

Three shrubs or sub-shrubs found in the grassland phase of many of these central Texas savanna communities are *Simsia calva* (Engelm. & A. Gray) A. Gray, (bush sunflower, Asteraceae), *Wedelia texana* (A. Gray) B. L. Turner, (= *Zexmenia hispida*, hairy wedelia, Asteraceae) and *Brickellia cylindracea* A. Gray and Engelm.,

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(brickell-bush, Asteraceae) (Correll and Johnston 1979; Enquist 1987; USDA 2009). These taxa are not reported from the woodlands or forest communities (Van Auken et al. 1979; Van Auken et al. 1980; Van Auken et al. 1981). They are usually not dominant but secondary species in these communities. They can be found at high density in some open habitats on dry, shallow soil in areas that have been disturbed (personal observation). They may be found at the edge of woodland or motts, but not below the canopy in these communities. They may require disturbances or low nutrient soils, but no studies were found concerning their requirements for establishment or their successional status. In addition, we have not found any studies of these species that might suggest limiting physiological factors or conditions. Physiological differences between plants native to open, full sun habitats compared to those found in shady, understory communities are fairly well known (Begon et al. 2006; Valladares and Niinemets 2008), but gas exchange rates of the species studied here have not been examined.

Sun plants usually have higher photosynthetic rates at high light levels, they light saturate at higher light levels, have higher light compensation points (photosynthetic rate equals respiration rate), higher dark respiration rates, higher transpiration rates and higher stomatal conductance rates compared to shade plants (Boardman 1977; Young and Smith 1980; Larcher 2003; Valladares and Niinemets 2008). Some species display what is called adaptive crossover and are capable of acclimating to high or low light environments, thus they could have a broader ecological niche (Givnish 1988; Givnish et al. 2004). Some plants, especially many trees start their growth in the low light environment of the canopy understory (Spurr and Barnes 1973), grow slowly for many years until they grow into a light gap. A light gap is created via a tree fall or plants reach the open, high light above the canopy (Ryniker et al. 2006; Van Auken and Bush 2009). In addition, shade leaves from plants grown in full sun have been used as surrogates for plants grown in shade conditions to understand a species' ecological requirements (Hamerlynck and Knapp 1994; Furuya and Van Auken 2009).

Gas exchange rates and other characteristics of sun and shade leaves of *Simsia calva*, *Wedelia texana* and *Brickellia cylindracea* were measured. Ambient light levels, xylem water potential and soil water content were also measured. Based on the habitats where these species were found, we expected that they were sun plants and would have higher maximum photosynthetic rates, light saturation points, light compensation points, respiration rates, conductance, and transpiration compared to shade-adapted species.

METHODS

Study Species

Simsia calva, (bush sunflower, Asteraceae), is a native, warm-season, perennial, sub-shrub with orange-yellow ray and disk flowers on long peduncles. It grows on disturbed, sand or heavy clay limestone soils and appears drought tolerant, widespread through central, southern, and southwestern Texas and southeastern New Mexico (Correll and Johnston 1979; Enquist 1987; Turner et al. 2003). *Wedelia texana* (= *Zexmenia hispida*, hairy wedelia, Asteraceae), is a native, warm-season, perennial, sub-shrub. It has bright yellow-orange flowers, blooming from March to December in South Texas, and May to September in central Texas (Correll and Johnston 1979; Enquist 1987). It is hardy, grows in disturbed areas and tolerates a variety of limestone soils (USDA 2009). It is found in central and west Texas and northeastern Mexico (Turner et al. 2003). *Brickellia cylindracea* (brickell-bush, Asteraceae), is a perennial, sub-shrub with considerable variability. Flowers are yellow, blooming from August through November (Correll and Johnston 1979; Enquist 1987). It is drought tolerant, has a strong preference for limestone soil, open habitats and is only found in central Texas (Turner et al. 2003).

Study Area

All plants in this field study were found on the southern edge of the Edwards Plateau region of central Texas just below the Balcones Escarpment in northern Bexar Co. (approximately 29° 68' N and 98° 50' W) (Correll and Johnston 1979; Van Auken et al. 1981; Van Auken and McKinley 2008; Furuya and Van Auken 2009). The Balcones Escarpment is rough, well-drained, with elevations increasing abruptly from approximately 200 m above mean sea level (AMSL) to 500 to 700 m AMSL. Most of the subsurface of the area is Cretaceous limestone, and soils are usually shallow, limestone derived, rocky or gravelly on slopes, and deep in broad valleys and flats (Taylor et al. 1962; NRCS 2006). Soils are dark colored, calcareous with usually neutral or slightly basic pH.

Area mean annual temperature is 20.0°C with monthly means ranging from 9.6°C in January to 29.4°C in July (NOAA 2004). Mean annual precipitation is 78.7 cm per year and bimodal, with peaks occurring in May and September (10.7 cm and 8.7 cm, respectively). There is little summer rainfall, high evaporation and high inter-annual variation (Thorntwaite 1931; NOAA 2004).

Juniperus-Quercus savanna or woodland is the major vegetation type in the study area and is representative of savannas and woodlands found throughout this region, but higher in woody plant

density than savanna communities farther to the west (Van Auken et al. 1979; Van Auken et al. 1980; Van Auken et al. 1981; Smeins and Merrill 1988). The high density woody species are *Juniperus ashei* J. Buchholz (Ashe juniper) and *Quercus virginiana* Mill. (= *Q. fusiformis* Small., live oak) followed by *Diospyros texana* Scheele. (Texas persimmon) and *Sophora secundiflora* (Ortega) DC. (Texas mountain laurel) with other oaks and elms in sheltered habitats or on deeper soil. Associated with these woodlands are relatively small grasslands and sparsely vegetated intercanopy patches or gaps (openings between the canopy trees) (Van Auken 2000). *Carex planostachys* Kunze (cedar sedge, Cyperaceae) (Wayne and Van Auken 2008) is the major herbaceous species below the canopy, but *Verbesina virginica* L. (frost weed, Asteraceae) is found in places on deeper soil (Gagliardia and Van Auken in press). In the grasslands and gaps *Aristida purpurea* Nutt. var. *longiseta* (Steud.) Vasey (red three-awn), *Bouteloua curtipendula* (Michx.) Torr. (side-oats grama), *Bothriochloa laguroides* (Steud.) Allred & Gould (silver bluestem), *B. ischaemum* (L.) Keng (KR bluestem), various other C₄ grasses, and a variety of herbaceous annuals are common (Van Auken 2000; USDA 2009).

Measurements

Gas exchange rates as a function of light level or photosynthetic flux density (PFD) were measured and plotted for sun and shade leaves of all three species (light response curves) (Hamerlynck and Knapp 1994; Furuya and Van Auken 2009). Five plants or replications were used. Individual sun and shade leaves were measured on each plant. All plants sampled were 0.5 to 1.0 m tall. All plants were growing in full sun. Sun leaves were on the outermost, southern facing canopy branches and shade leaves were on the lower, innermost branches of these plants. Shade leaves from full sun plants were used as surrogates for shade plants as reported by others (Hamerlynck and Knapp 1994; Furuya and Van Auken 2009).

Light response measurements were made in June within ± 3 hr of solar noon with a LI-COR® infrared gas analyzer (LI-6400). Irradiances were generated by the LI-COR LED red-blue light source using a light curve program with the LI-COR, a gas flow rate of 400 $\mu\text{mol/s}$, and a CO₂ concentration of 400 $\mu\text{mol/mol}$. One mature, undamaged, fully expanded leaf per replication and leaf type was used with the 2×3 cm chamber. The LI-COR 6400 was run at approximate ambient summer, midday, daytime temperature (35°C) and relative humidity (50%), and was calibrated daily. All response data were recorded after at least two minutes when a stable

total coefficient of variation was reached ($<0.3\%$), usually less than five minutes. All light response curves were started at a PFD of 2000 $\mu\text{mol/m}^2/\text{s}$ for sun leaves and shade leaves and then decreased to the following: 1800, 1400, 1200, 1000, 800, 600, 400, 200, 100, 75, 50, 25, 10, 5, and 0 $\mu\text{mol/m}^2/\text{s}$ (16 total measurements).

Measurements for each species and leaf type included net photosynthesis, stomatal conductance, and transpiration. Repeated measure ANOVA was utilized to determine if significant differences occurred between leaf types. A one way ANOVA was used to determine if net photosynthesis, stomatal conductance, and transpiration were significantly different between the PFD's tested and also between leaf types (Sall et al. 2001). If significant differences were found within a leaf type, Tukey-Kramer Honestly Significant Difference test was used to determine where significant differences occurred. Shapiro-Wilks tests were used to test for normal distributions and the Bartlett's test was used to test for homogeneity of variances. Data were log transformed for analyses due to unequal variances as necessary.

Maximum photosynthesis (A_{max}), PFD at A_{max} , transpiration at A_{max} , conductance at A_{max} , light saturation point, dark respiration, light compensation point, and the quantum yield efficiency (initial slope) were determined for each replicate, and means were calculated. The A_{max} was the highest net photosynthesis rate. Light saturating photosynthesis was the PFD when the slope of the initial rate line reached the A_{max} . Dark respiration was the gas exchange rate at a PFD of 0 $\mu\text{mol/m}^2/\text{s}$ (y-intercept of the line for the initial slope or rate). The light compensation point was calculated as the PFD when the photosynthetic rate = 0 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ (x-intercept of the line for the initial slope or rate). The quantum yield efficiency or initial slope was calculated using the dark value and increasing PFDs until the regression coefficient of the slope decreased (150 $\mu\text{mol/m}^2/\text{s}$ PFD) (Furuya and Van Auken 2009; Wayne and Van Auken 2009).

A one-way ANOVA (Sall et al. 2001) was used to detect significant difference between species and between leaf types for maximum photosynthetic rates (A_{max}), light saturation, dark respiration, transpiration at A_{max} , conductance at A_{max} , and quantum yield efficiency. Significance level for all tests was 0.05. Ambient PFD was also measured for each sun and shade leaf with the LI-COR® integrating quantum sensor at the time the light response curves were initiated (LI-COR, Inc, Lincoln, NE).

Pre-dawn Xylem Water Potential (Ψ_x)

Measurements of pre-dawn xylem water potential were made for leaves of each plant

(Scholander et al. 1965; Furuya and Van Auken 2009) with the model 1000 PMS® pressure chamber (PMS, Instrument, Co. Corvallis, OR). Samples of each leaf type were collected with a sharp knife and put in a zip lock plastic bag with a wet paper towel between 4:30 and 5:00 a.m. The plastic bag was put in a cooler with ice to insure that Ψ_x would not change. Ψ_x measurements were made within 45 min of harvest. A one-way ANOVA (Sall et al. 2001) was used to detect significant difference between species and between leaf types.

Soil Moisture Measurements

Volumetric soil moisture measurements were made using time domain reflectometry (TDR) with a TRIME portable TDR soil moisture meter (TRIME-FM) (MESA System Co. Medfield, ME). The TDR is a transmission line technique used to determine soil water content by inserting two parallel metal rods in a soil matrix to make measurements (Topp and Reynolds 1998; Noborio 2001). Soil water content was measured in five positions below the canopy of each plant. The five positions were the four cardinal compass points and the site next to the bole of the plant. Soil water content of 5 plants was sampled between 10:00 and 11:00 a.m. The site next to the bole of the plant was on the south side, and the other locations were approximately 10 cm from the bole. Data from 5 sites (north, south, east, west, and the site next to the plant) around each plant were pooled and a mean and standard error was determined. A one-way ANOVA (Sall et al. 2001) was used to detect significant difference between species.

Leaf Area and Total Leaf Dry Mass

Area (LA) and total dry mass (Mooney and Gulmon 1982) of five sun and five shade leaves were measured to determined mass per unit area (LMA) (g/cm²). The sun and shade leaves used to make gas exchange measurements were collected after gas exchange measurements were completed and used to determine leaf area and total dry mass. Leaves were dried at 60C to a constant mass prior to weighing. A one-way ANOVA (Sall et al. 2001) was used to detect significant difference between species and between leaf types.

RESULTS

The photosynthetic light response curves for the sun and shade leaves were significantly different over the light levels measured for all three species (Repeated Measures ANOVA, $P < 0.05$; Fig. 1A, B, C). At PFD's above 400–600 $\mu\text{mol}/\text{m}^2/\text{s}$ (depending on the species), sun leaves had significantly higher photosynthetic rates than

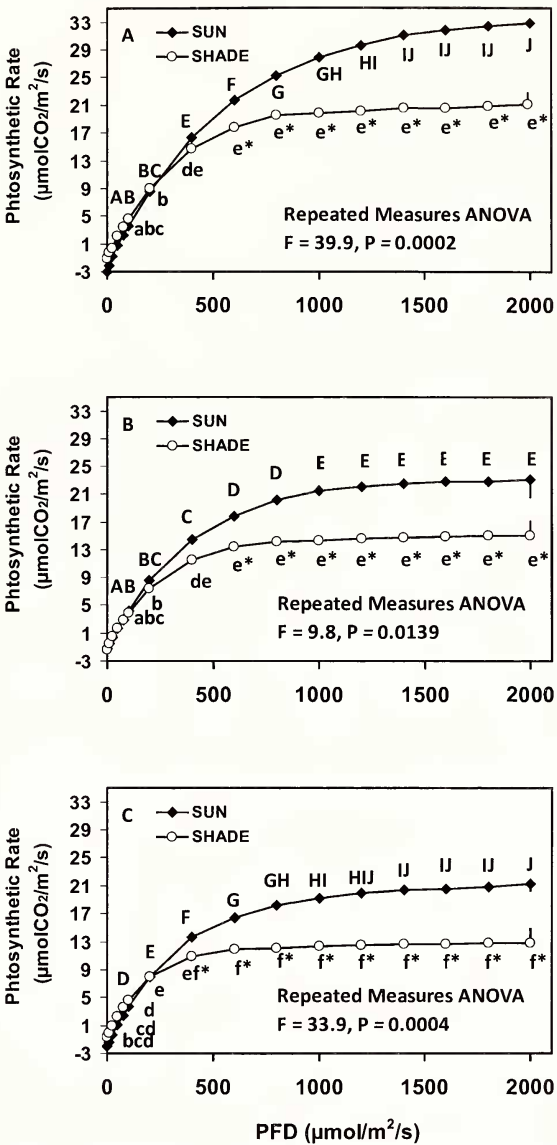


FIG. 1. Photosynthetic light response curves for sun (◆) and shade (○) leaves of (A) *Simsia calva*, (B) *Wedelia texana* and (C) *Brickellia cylindracea*. There were significant differences in photosynthetic rates for sun and shade leaves of the three species (repeated measures ANOVA, $P < 0.05$). Error bars are examples and represent + or – one standard error of the mean. Different letters between light levels indicate significant differences between sun leaves (upper case) or shade leaves (lower case) and between leaf types (*). Rates were not significantly different for sun leaves between PFD's of zero and 100 $\mu\text{mol}/\text{m}^2/\text{s}$ or shade leaves either for *S. calva* or *W. texana*. There were significant but small differences in rates for *B. cylindracea* over the same range.

shade leaves, while at PFD's lower than 400–600 $\mu\text{mol}/\text{m}^2/\text{s}$, shade leaves generally had higher rates than sun leaves. Photosynthetic rates for the sun leaves continued to increase from 400–600 to

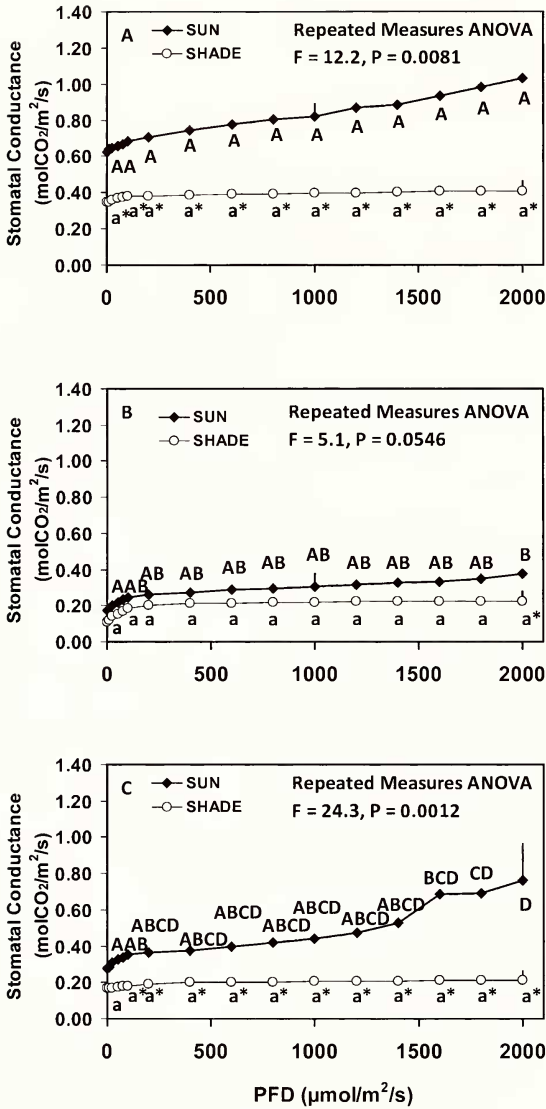


FIG. 2. Stomatal conductance curves for sun (◆) and shade (○) leaves of (A) *Simsia calva*, (B) *Wedelia texana* and (C) *Brickellia cylindracea*. There were significant differences in stomatal conductance rates for sun and shade leaves of each species (repeated measures ANOVA, $P < 0.05$). Error bars are examples and represent + or - one standard error of the mean. Different letters between light levels indicate significant differences between sun leaves (upper case) or shade leaves (lower case) and between leaf types (*). Rates were not significantly different for sun leaves between PFD's of zero and 100 $\mu\text{mol}/\text{m}^2/\text{s}$ or shade leaves either for any of the three species.

2000 $\mu\text{mol}/\text{m}^2/\text{sec}$, with few significant differences (Fig. 1A, B, C). The same was true for the shade leaves.

Stomatal conductance of the sun and shade leaves were significantly different over the light levels examined (Repeated Measures ANOVA, $P < 0.05$; Fig. 2A, B, C). However, there were

few significant differences between light levels for sun or shade leaves over the light levels tested (One way ANOVA). When significant differences were detected, they were usually at the lowest light levels examined. The sun leaves had higher conductance rates at most light levels tested, but they were not always significantly different. Transpiration rates of the two leaf types (sun and shade) were also significantly different over the light levels measured for all three species (Repeated Measures ANOVA; $F = 6.6$, $P = 0.0245$; $F = 10.7$, $P = 0.0112$, $F = 16.9$, $P = 0.0034$). At all light levels tested, the transpiration rate was significantly higher for the sun leaves compared to shade leaves for *W. texana* and *B. cylindracea*. For *S. calva*, transpiration rates were higher for sun leaves at all light levels tested, but differences were significant only at the two highest and the two lowest light levels (data not presented). Transpiration rates were 1–2% of the conduction rates (Table 1).

The maximum photosynthetic rate (A_{max}) of *S. calva* sun leaves was 32.8 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ (Fig. 3A) and occurred at the maximum PFD (light level) measured (2000 $\mu\text{mol}/\text{m}^2/\text{s}$). This rate was 1.41 times higher than the A_{max} rate for sun leaves of *W. texana* and 1.55 times the rate for sun leaves of *B. cylindracea*. *Simsia calva* also had the highest A_{max} for shade leaves at 21.3 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$. This rate was significantly higher than the rates for the other two species. The A_{max} for the sun leaves of all three species was significantly higher than their respective shade leaves (Fig. 3A). The A_{max} rates for the shade leaves was 61–66% of the rates for the sun leaves at PFDs of 1400 or 1600 $\mu\text{mol}/\text{m}^2/\text{s}$. Ambient light levels were significantly different for the two leaf types, with the sun leaves being exposed to 6.1–8.8 times more light (Fig. 3A). There were no species differences in exposure to ambient full sun or shade.

Light saturation (L_{sat}) for sun leaves of *S. calva* was 672 $\mu\text{mol}/\text{m}^2/\text{s}$, which was significantly higher than the L_{sat} for *B. cylindracea* but not *W. texana* (Fig. 3B). The L_{sat} for the sun leaves of all three species was higher than the shade leaves of the respective species. *Brickellia cylindracea* shade leaves had the lowest L_{sat} (260 $\mu\text{mol}/\text{m}^2/\text{s}$). The light compensation point (L_{cp}) of sun leaves of all three species was not significantly different and was between 18 and 39 $\mu\text{mol}/\text{m}^2/\text{sec}$ (Fig. 3B). The L_{cp} of shade leaves was similar with only *B. cylindracea* having a significantly lower value at 10 $\mu\text{mol}/\text{m}^2/\text{s}$ (Fig. 3B).

The dark respiration (R_d) of sun leaves was not significantly different, ranging from 1.3–3.0 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ (Table 1). The R_d of shade leaves was not significantly different ranging from 0.7–1.1 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$. The only significant difference between sun and shade leaves was for *B. cylindracea* and the R_d was 35% of the value for the sun leaves. The mean (± 1 SE) quantum yield

TABLE 1. PHYSIOLOGICAL MEASUREMENTS (MEANS AND ONE STANDARD ERROR, SE) FOR SUN AND SHADE LEAVES OF *S/MISIA CALI'A* (SC), *W/EDELIA TEXANA* (WT) AND *BRICKELLIA CYLINDRICEA* (BC) AS WELL AS SOIL WATER CONTENT AND LEAF CHARACTERISTICS. Means for the same parameter and the same leaf type with the same upper case letter are not significantly different at the 0.05 level (one-way-ANOVA, Tukey-Kramer honestly Significant Difference test). Means for the same parameter and the same species followed with the same lower case letter are not significantly different at the 0.05 level (one-way-ANOVA).

Parameter	Leaf type/species mean (SE)			
	Sun leaves		Shade leaves	
	SC	WT	BC	SC
g_{leaf} – conductance (molH ₂ O/m ² /s) at A_{max}	1.02 Aa (0.14)	0.36 Ba (0.05)	0.76 ABa (0.21)	0.40 Ab (0.04)
E_{leaf} – transpiration (mmolH ₂ O/m ² /s) at A_{max}	9.0 Aa (1.1)	6.5 ABa (0.5)	5.9 Ba (0.6)	5.3 Ab (0.2)
R_d – dark respiration (μmolCO ₂ /m ² /s)	3.0 Aa (0.8)	1.3 Aa (0.4)	2.0 Aa (0.3)	1.1 Aa (0.3)
LA (cm ²) – leaf area	8.4 Bb (0.7)	7.3 Ba (0.4)	19.4 Aa (1.0)	13.6 Ba (0.9)
LM (g) – leaf mass	0.053 Aa (0.001)	0.043 Aa (0.004)	0.074 Aa (0.004)	0.061 Aa (0.001)
LMA (g/cm ²) – Mass/area	0.0063 Aa (0.0004)	0.0059 Aa (0.0003)	0.0038 Ba (0.0001)	0.0045 Ab (0.0004)
Ψ _x (Mpa) – leaf water potential	–0.58 Ba (0.14)	–1.84 Aa (0.19)	–0.65 Ba (0.05)	–0.70 Ba (0.14)
Soil moisture (%)	11.7 A (0.77)	14.1 A (0.91)	16.1 A (1.76)	–1.78 Aa (0.07)
				0.0028 Bb (0.0002)
				–0.44 Ba (0.10)
				2.7 Bb (0.4)
				0.7 Ab (0.1)
				21.0 Aa (0.8)
				0.058 Ab (0.006)
				0.0046 Ab (0.0004)
				–1.78 Aa (0.07)
				0.22 Bb (0.02)
				0
				.21 Bb (0.03)

efficiency or the initial slope (QY or IS) (slope of the line from 0–150 $\mu\text{mol}/\text{m}^2/\text{s}$) was 0.041 ± 0.009 to 0.061 ± 0.013 and not significantly different between the species for sun or shade leaves (data not shown).

Conductance at A_{\max} was significantly higher for sun leaves compared to shade leaves for all three species. *Simsia calva* had the highest conductance rate for sun or shade leaves of all three species. Transpiration rates were similar with higher rates for sun leaves compared to shade leaves and *S. calva* had the highest rates and *B. cylindracea* had the lowest rates (Table 1).

Brickellia cylindracea had the largest leaf area (LA) for sun and shade leaves and there were no significant differences in sun and shade LA except for *S. calva*, which had larger shade leaves. Shade leaves of *B. cylindracea* were larger than the shade leaves of the other two species and shade leaves of *W. texana* were smallest. There were no significant differences in the sun leaf mass for any of the species (Table 1). The leaf mass/area (LMA) for *B. cylindracea* sun and shade leaves was significantly lower than the other species and all three species shade leaves had lower LMA than their respective sun leaves.

The xylem water potential (Ψ_x) of the sun and shade leaves was not significantly different, but *W. texana* had the most negative Ψ_x at -1.84 MPA for sun leaves. The surface soil was dry, having only 11.7–16.1% soil moisture and no significant differences between species.

DISCUSSION

All three of the species studied are commonly found growing in high light environments in Central Texas savannas, but not in shaded habitats (Van Auken et al. 1981; Enquist 1987), and sun leaves of all three species had high maximum photosynthetic rates (A_{\max}), typical of species of open habitats (Begon et al. 2006) (Fig. 3). Other photosynthetic parameters, including light saturation, light compensation, dark respiration, conductance, and transpiration, were high for sun adapted leaves (Fig. 3, Table 1). However, shade leaves had relatively high gas exchange parameters as well, probably because of the relatively open nature of the sub-shrub canopy and the presence of light flecks (Hull 2002). These responses are not consistent with findings for shade plants, but for plants that are sun plants or intermediate or facultative species (Boardman 1977; Hull 2002; Larcher 2003; Givnish et al. 2004; Begon et al. 2006; Valladares and Niinemets 2008). Although *Simsia calva*, *Wedelia texana* and *Brickellia cylindracea* are all native species with a fairly broad distribution in central Texas, west Texas, New Mexico and northern Mexico, very little is known about their photosynthetic capabilities. No studies were

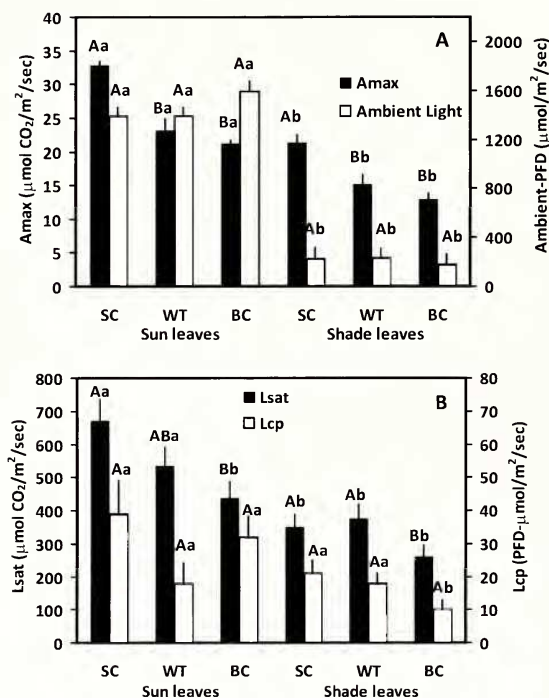


FIG. 3. Mean A_{\max} values + one standard error (A) and ambient light levels (PFD) for sun and shade leaves of *Simsia calva* (SC), *Wedelia texana* (WT) and *Brickellia cylindracea* (BC). Mean light saturation (L_{sp}) + one standard error (B) and light compensation point (L_{cp}) for the same species. Bars for the same parameter and the same leaf type with the same upper case letter are not significantly different at the 0.05 level (one-way-ANOVA). Bars for the same parameter and the same species followed with the same lower case letter are not significantly different at the 0.05 level (one-way-ANOVA, Tukey-Kramer honestly Significant Difference test).

identified which evaluated their physiological responses or growth responses to light levels or other factors. The parameters measured for both leaf types suggest that these species are sun or facultative species, because some individuals may be found in partial shade or at the edge of woodland canopies or in light gaps (personal observation).

In general, true understory species have much lower photosynthetic rates than the rates reported for the three species in the current study. Photosynthetic rates of three understory montane spruce forests species found in central Europe had CO₂ uptake rates of 3.4–5.5 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ (Hättenschwiler and Körner 1996). In addition, the European forest species reached light saturation at lower light levels ($\sim 200 \mu\text{mol}/\text{m}^2/\text{s}$) than sun leaves of the species reported here (435–672 $\mu\text{mol}/\text{m}^2/\text{s}$). Even shade leaves of *S. calva*, *W. texana* and *B. cylindracea* light saturated at higher light levels (260–375 $\mu\text{mol}/\text{m}^2/\text{s}$) than the forest understory species. *Arnica cordifolia* Hook.

(Asteraceae), an herbaceous perennial which grows in the understory of lodgepole pine forests in southeastern Wyoming, also had photosynthetic rates (3.5–4.2 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$) that were 18–30% of the rates of shade adapted leaves of the species in the current study and reached light saturation at light levels at about the same levels as shade leaves in the current study ($\sim 330 \mu\text{mol CO}_2/\text{m}^2/\text{s}$) (Young and Smith 1980).

Polygonum virginianum L. (Polygonaceae), found in the forest understory and at the forest edge in the eastern United States, had an A_{\max} of $\sim 3 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ at a light saturation of $\sim 500 \mu\text{mol}/\text{m}^2/\text{s}$ (Zangerl and Bazzaz 1983). *Carex planostachys* from the central Texas Edwards Plateau *Juniperus* woodland understory had an A_{\max} value of $4.9 \pm 0.3 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ which was 23.0–38.0% of the value for shade leaves of the three species in the current study. In addition, light saturation for *C. planostachys* was about half the value of the current species studied at $151 \pm 43 \mu\text{mol}/\text{m}^2/\text{s}$ (Wayne and Van Auken 2009). While *S. calva*, *W. texana* and *B. cylindracea* are typically found growing in open habitats and sometimes at the edge of woodlands, their high A_{\max} for shade adapted leaves compared to other herbaceous shade plants would suggest they are sun species, and would not grow in low light environments.

True sun plants are adapted to high light conditions and consequently have high rates of gas exchange. For example, an early successional herbaceous perennial, *Abutilon theophrasti* Medik., had A_{\max} rates between 15–25 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ (Wieland and Bazzaz 1975; Bazzaz 1979; Munger et al. 1987a, b; Hirose et al. 1997; Lindquist and Mortensen 1999; Van Auken and Bush (in press). Two oaks found mostly in gallery forest in tall grass prairies of northeastern Kansas, *Quercus muehlenbergii* Engelm. and *Q. macrocarpa* Michx. had A_{\max} rates of 18–26 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ for sun leaves and 11–13 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ for shade leaves (Hamerlynck and Knapp 1994).

Some plants, particularly early successional species or plants from disturbed (open) communities can acclimate to variability of the light environment in which they live (Bazzaz and Carlson 1982). For example, *Polygonum pensylvanicum* L., a colonizing annual of open fields, had an A_{\max} of $\sim 12 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ at $\sim 1500 \mu\text{mol}/\text{m}^2/\text{s}$ when plants from a shaded-habitat (200 $\mu\text{mol}/\text{m}^2/\text{s}$) were measured (Bazzaz and Carlson 1982; Zangerl and Bazzaz 1983). However, the rate was $\sim 24 \mu\text{mol}/\text{m}^2/\text{s}$ at $\sim 1800 \mu\text{mol}/\text{m}^2/\text{s}$ when plants from a full sun habitat were examined (Bazzaz and Carlson 1982). The light levels of the sun leaves we reported in the present study received 1389 ± 83 to $1594 \pm 103 \mu\text{mol}/\text{m}^2/\text{s}$ (~ 65 –80% full sunlight). Individuals from higher light environments could have higher maximum photosynthetic rates, while those from lower light

environments would probably be lower. Further studies would be needed to determine if these species acclimate to variability in the light environment as reported for other species (Hull 2002; Valladares and Niinemets 2008).

Dark respiration of sun leaves of *S. clava* ($3.0 \pm 0.8 \mu\text{mol CO}_2/\text{m}^2/\text{s}$) are similar to other sun-adapted plants (Hamerlynck and Knapp 1994). This rate is 2.72 times higher than the R_d of its shade adapted leaves. The R_d for shade adapted leaves of all three species examined is about five times higher than rates for true shade adapted species (Hirose and Bazzaz 1998; Hull 2002). Dark respiration for shade-adapted species is typically lower than sun-adapted species, due to the lower metabolism of shade-adapted plants (Bjorkman 1968; Bazzaz and Carlson 1982). *P. pensylvanicum* grown at $200 \mu\text{mol}/\text{m}^2/\text{s}$ had a respiration rate of $\sim 0.5 \mu\text{mol CO}_2/\text{m}^2/\text{s}$, and the rate for sun leaves was twice this level (Bazzaz and Carlson 1982).

Values of other photosynthetic parameters reported in this study for the three savanna subshrubs are similar to those reported for sun plants or sun leaves from the literature. Quantum yield efficiency reported here ($0.041\text{--}0.061 \mu\text{mol CO}_2/\mu\text{mol quanta}$, sun leaves and shade leaves) are within the range or similar to values reported for other species ($0.035\text{--}0.052 \mu\text{mol CO}_2/\mu\text{mol quanta}$) (Hirose et al. 1997). Stomatal conductance and transpiration reported from the species in the current study were similar to other studies and indicate open stomates; however, many factors affect the levels of these parameters (Wieland and Bazzaz 1975; Zangerl and Bazzaz 1984; Yun and Taylor 1986; Munger et al. 1987a, b; Stafford 1989).

The sun and shade leaves of *S. calva*, *W. texana* and *B. cylindracea* have relatively high gas exchange rates. These physiological responses to various light levels more than likely are contributors to the niche observed for this species. In the field they are usually found in disturbed grasslands, gaps and other high light environments. In general, resource utilization is spatially partitioned among species along complex environmental gradients, such as changes in light from open areas to woodland or forest edges (Van Auken and Bush 2009; Wayne and Van Auken 2009; Gagliardia and Van Auken in press). The ability of these three species to reach high photosynthetic rates in partial shade and having relatively low light compensation points would allow them to exist at the canopy edge or in partially shaded savanna communities. At light levels below approximately $400 \mu\text{mol CO}_2/\text{m}^2/\text{s}$, more shade tolerant species would probably be able to out-compete these three sub-shrubs. At light levels above $400\text{--}500 \mu\text{mol CO}_2/\text{m}^2/\text{s}$, *S. calva*, *W. texana* and *B. cylindracea* could be community dominants and out-compete other co-

occurring species, especially in disturbed areas or in areas where grass biomass and density is reduced because of heavy grazing and a low fire frequency. This would occur in part because they have photosynthetic rates as high as or higher than most co-occurring species (Grunstra 2008; Valladares and Niinemets 2008).

These central Texas savannas have apparently changed considerably over the past 200+ years for a number of reasons (Van Auken and McKinley 2008; Van Auken and Smeins 2008). Recently, heavy grazing, tree cutting and reduced fire frequency have been major factors contributing to community alterations. These are proximate factors, but they are not the only factors. Some still blame global climatic changes, including elevated CO_2 levels and increased temperature levels, but these factors appear to be background conditions and not the conditions directly causing the decrease in many native grasses (Van Auken 2009). We expect that these three sub-shrubs have increased in density, cover and possibly range because of the reduction in grass biomass because of herbivory and the lack of grassland fires and their apparent resistance to both native and domestic herbivory.

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LITERATURE CITED

BAZZAZ, F. A. 1979. The physiological ecology of plant succession. *Annual Review of Ecology and Systematics* 10:351–371.

——— AND R. W. CARLSON. 1982. Photosynthetic acclimation to variability in the light environment of early and late successional plants. *Oecologia* 54:313–316.

BEGON, M., C. R. TOWNSEND, AND J. L. HARPER. 2006. *Ecology: from individuals to ecosystems*. Blackwell Publishing, Malden, MA.

BJORKMAN, O. 1968. Carboxydismutase activity in shade-adapted and sun-adapted species of higher plants. *Physiologia Plantarum* 21:1–10.

BOARDMAN, N. K. 1977. Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Physiology* 28:355–377.

BOND, W. J. 2008. What limits trees in C_4 grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics* 39:641–659.

BRESHEARS, D. D. 2008. Structure and function of woodland mosaics: consequences of patch-scale heterogeneity and connectivity along the grassland-forest continuum. Pp. 58–92 in O. W. Van Auken (ed.), *Western North American Juniperus communities: a dynamic vegetation type*. Springer, New York, NY.

CORRELL, D. S. AND M. C. JOHNSTON. 1979. *Manual of the vascular plants of Texas*. The University of Texas at Dallas, Richardson, TX.

- ENQUIST, M. 1987. Wildflowers of the Texas Hill Country. Lone Star Botanical, Austin, TX.
- FURUYA, M. AND O. W. VAN AUKEN. 2009. Gas exchange rates of sun and shade leaves of *Sophora secundiflora*. Texas Journal of Science 61:243–258.
- GAGLIARDIA, J. W. AND O. W. VAN AUKEN. In Press. Distribution of *Verbesina virginica* (Asteraceae, Frost Weed) in Central Texas and possible causes. Texas Journal of Science 62.
- GIVNISH, T. J. 1988. Adaptation to sun and shade - a whole-plant perspective. Australian Journal of Plant Physiology 15:63–92.
- , R. A. MONTGOMERY, AND G. GOLDSTEIN. 2004. Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant compensation points. American Journal of Botany 91: 228–246.
- GRUNSTRA, M. B. 2008. Investigation of *Juniperus* woodland replacement dynamics Ph. D. Dissertation. University of Texas at San Antonio, TX.
- HAMERLYNCK, E. P. AND A. K. KNAPP. 1994. Leaf-level responses to light and temperature in two co-occurring *Quercus* (Fagaceae) species: implications for tree distribution patterns. Forest Ecology and Management 68:149–159.
- HÄTTENSCHWILER, S. AND C. KÖRNER. 1996. Effects of elevated CO₂ and increased nitrogen deposition on photosynthesis and growth of understory plants in spruce model ecosystems. Oecologia 106: 172–180.
- HIROSE, T., D. D. ACKERLY, M. B. TRAW, D. RAMSEIER, AND F. A. BAZZAZ. 1997. CO₂ elevation, canopy photosynthesis, and optimal leaf area index. Ecology 78:2339–2350.
- AND F. A. BAZZAZ. 1998. Trade-off between light- and nitrogen-use efficiency in canopy photosynthesis. Annals of Botany 82:195–202.
- HOUSE, J. I., S. R. ARCHER, D. D. BRESHEARS, AND R. J. SCHOLES. 2003. Conundrums in mixed woody-herbaceous plant systems. Journal of Biogeography 30:1763–1777.
- HULL, J. C. 2002. Photosynthetic induction dynamics to sunflecks of four deciduous forest understory herbs with different phenologies. International Journal of Plant Sciences 163:913–924.
- LARCHER, W. 2003. Physiological plant ecology: ecophysiology and stress physiology of functional groups. Springer, New York, NY.
- LINDQUIST, J. L. AND D. A. MORTENSEN. 1999. Ecophysiological characteristics of four maize hybrids and *Abutilon theophrasti*. Weed Research 39:271–285.
- MAZE, D. M. 2009. Effect of terrestrial mollusc herbivory on *Holocarpha macradenia* (Asteraceae) seedlings in California coastal prairie under different clipping regimes. Madroño 56:1–7.
- MOONEY, H. A. AND S. L. GULMON. 1982. Constraints on leaf structure and function in reference to herbivory. BioScience 32:198–206.
- MUNGER, P. H., J. M. CHANDLER, AND J. T. COTHREN. 1987a. Effect of water stress on photosynthetic parameters of soybean (*Glycine max*) and velvetleaf (*Abutilon theophrasti*). Weed Science 35:15–21.
- , ———, AND F. M. HONS. 1987b. Soybean (*Glycine max*) - velvetleaf (*Abutilon theophrasti*) interspecific competition. Weed Science 35:647–653.
- NOAA. 2004. Meteorological data. National Climatic Data Center, National Oceanic and Atmospheric Administration. Website <http://www.ncdc.noaa.gov/oa/ncdc.html> [accessed 19 August 2010].
- NOBORIO, K. 2001. Measurement of soil water content and electrical conductivity by time domain reflectometry: a review. Computers and electronics in agriculture 31:213–237.
- NRCS. 2006. Web Soil Surveys. Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Website <http://websoilsurvey.nrcs.usda.gov/app/> [accessed 19 August 2010].
- RYNIKER, K. A., J. K. BUSH, AND O. W. VAN AUKEN. 2006. Structure of *Quercus gambelii* communities in the Lincoln National Forest, New Mexico, USA. Forest Ecology and Management 233:69–77.
- SALL, J., A. LEHMAN, AND L. CREIGHTON. 2001. JMP start statistics: a guide to statistics and data analysis using JMP and JMP IN software. Duxbury Thomson Learning, Pacific Grove, CA.
- SCHOLANDER, P. F., H. T. HAMMEL, E. D. BRADSTREET, AND F. A. HEMMINGSEN. 1965. Sap pressure in vascular plants. Science 148:339–346.
- SMEINS, F. E. AND L. B. MERRILL. 1988. Long-term change in semi-arid grasslands, Pp. 101–114 in B. B. Amos and F. R. Gehlbach, (eds.), Edwards Plateau vegetation: plant ecological studies in central Texas. Baylor University Press, Waco, TX.
- SPURR, S. H. AND B. V. BARNES. 1973. Forest ecology. The Roland Press, New York, NY.
- STAFFORD, R. A. 1989. Allocation responses of *Abutilon theophrasti* to carbon and nutrient stress. American Midland Naturalist 121:225–231.
- TAYLOR, F. B., R. B. HAILEY, AND D. L. RICHMOND. 1962. Soil survey of Bexar County, Texas. United States Department of Agriculture. Soil Conservation Service, Washington D.C.
- THORNTWHAITE, C. W. 1931. The climates of North America: according to a new classification. Geographical Review 21:633–655.
- TOPP, G. C. AND W. D. REYNOLDS. 1998. Time domain reflectometry: a seminal technique for measuring mass and energy in soil. Soil tillage research 47:125–132.
- TURNER, B. L., H. NICHOLS, G. DENNY, AND O. DORON. 2003. Atlas of vascular plants of Texas. Brit Press, Fort Worth, TX.
- USDA, NRCS. 2009. The PLANTS Database, National Plant Data Center, Baton Rouge, LA. Website <http://plants.usda.gov/index.html>. [accessed 13 August 2010].
- VALLADARES, F. AND U. NIINEMETS. 2008. Shade tolerance, a key plant feature on complex nature and consequences. Annual Review of Ecology and Systematics 39:237–257.
- VAN AUKEN, O. W. 2000. Characteristics of intercanopy bare patches in *Juniperus* woodlands of the southern Edwards Plateau, Texas. Southwestern Naturalist 45:95–110.
- . 2009. Causes and consequences of woody plant encroachment into western North American grasslands. Journal of Environmental Management 90:2931–2942.

——— AND J. K. BUSH. 2009. Gas exchange rates of *Quercus gambelii* in *Q. gambelii* woodlands. *Journal of the Torrey Botanical Society* 136:465–478.

——— AND ———. In Press. Photosynthetic rates of two species of Malvaceae, *Malvaviscus arboreus* var. *drummondii* (Wax mallow) and *Abutilon theophrasti* (Velvetleaf). *Southwestern Naturalist* 56.

——— AND D. C. MCKINLEY. 2008. Structure and composition of *Juniperus* communities and factors that control them, Pp. 19–47 in O. W. Van Auken (ed.), *Western North American Juniperus communities: a dynamic vegetation type*. Springer, New York.

——— AND F. SMEINS. 2008. Western North American *Juniperus* communities: patterns and causes of distribution and abundance, Pp. 3–18 in O. W. Van Auken (ed.), *Western North American Juniperus communities: a dynamic vegetation type*. Springer, New York, NY.

———, A. L. FORD, AND J. L. ALLEN. 1981. An ecological comparison of upland deciduous forests of central Texas. *American Journal of Botany* 68:1249–1256.

———, ———, AND A. G. STEIN. 1979. A comparison of some woody upland and riparian plant communities of the southern Edwards Plateau. *Southwestern Naturalist* 24:165–180.

———, ———, A. STEIN, AND A. G. STEIN. 1980. Woody vegetation of upland plant communities in the southern Edwards Plateau. *Texas Journal of Science* 32:23–35.

WAYNE, E. R. AND O. W. VAN AUKEN. 2008. Comparisons of the understory vegetation of *Juniperus* woodlands, Pp. 93–110 in O. W. Van Auken (ed.), *Western North American Juniperus communities: a dynamic vegetation type*. Springer, New York, NY.

——— AND ———. 2009. Light responses of *Carex planostachys* from various microsites in a *Juniperus* community. *Journal of Arid Environments* 73:435–443.

WIELAND, N. K. AND F. A. BAZZAZ. 1975. Physiological ecology of three codominant successional annuals. *Ecology* 56:681–688.

YOUNG, D. R. AND W. K. SMITH. 1980. Influence of sunlight on photosynthesis, water relations, and leaf structure in the understory species *Arnica cordifolia*. *Ecology* 61:1380–1390.

YUN, J. I. AND S. E. TAYLOR. 1986. Adaptive implications of leaf thickness for sun- and shade-grown *Abutilon theophrasti*. *Ecology* 67:1314–1318.

ZANGERL, A. R. AND F. A. BAZZAZ. 1983. Plasticity and genotypic variation in photosynthetic behaviour of an early and a late successional species of *Polygonum*. *Oecologia* 57:270–273.

——— AND ———. 1984. Effects of short-term selection along environmental gradients on variation in populations of *Amaranthus retroflexus* and *Abutilon theophrasti*. *Ecology* 65:207–217.